

LARVAL DEVELOPMENT OF PALAEMONETES PUGIO HOLTHUIS^{1, 2}

A. C. BROAD

Duke University Marine Laboratory, Beaufort, N.C.

Knowledge of the larval development of the marine species of *Palaemonetes* of the eastern United States is limited to Faxon's (1879) account of the development of *P. vulgaris*. This study was based almost wholly on planktonic larvae collected in an area from which two other closely related species, *P. pugio* and *P. intermedius*, have been described since (Holthuis, 1949). Holthuis (1952) feels that even mature adults of these species often have been confused. The larvae, presumably, may be quite similar, although those of the two latter species are unknown.

The problem of distinguishing between decapod species during the larval phase has received relatively little attention. Lebour (1927 through 1943) has found generic, and in some instances specific, taxonomic characters for British decapod larvae, but sometimes only was able to state that larvae of certain species were alike. Gurney (1942) feels that similarity between larvae indicates the relationship between the species. Often larvae of commercially valuable decapods have been studied without consideration of the larvae of related species. Churchill's (1942) account of the zoeae of the blue crab, *Callinectes sapidus*, is thought by Hopkins (1944) to include larvae of another species, possibly *C. ornatus*. Pearson's (1939) description of the development of the white shrimp, *Penaeus setiferus*, has been questioned by Burkenroad (1949) and Heegaard's (1953) descriptions of larvae of the same species are thought by Gunter (editorial comment in Heegaard, 1953) to include larvae of other penaeids.

Among species most studied there has been relatively little agreement on either the form or the number of larval stages. Churchill (1942) found five blue crab zoeae. Hopkins (1943, 1944) found four, but feels that a fifth may exist which has never been found. Sandoz and Rogers (1944) obtained a pre-zoeal blue crab in the laboratory which has not been found in nature. Heegaard (1953) questions the number of white shrimp stages found by Pearson (1939). The number of naupliar stages reported for other species of *Penaeus* varies still more (Hudinaga, 1942; Heldt, 1938). Many of these accounts were based on larvae caught in plankton and have been questioned. The validity of a reconstruction depends upon the ability of the author to recognize species during the larval phase. The difficulty is apparent, especially when another closely related species may exist in the same region.

Intraspecific variation in development among euphausiids has been fairly well established (MacDonald, 1927; Fraser, 1936; Boden, 1950, 1951), but variation

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in decapod larvae has been denied (Gurney, 1942). Heegaard (1953), however, feels that, at least among penaeids, variation in the rate of larval development may result in differences in the number and form of larval intermolts for each species. Some doubt may have been cast on this hypothesis by the paucity and questionable identity of the material on which it was based. The pre-zoeal stage of *Callinectes* reported by Sandoz and Rogers (1944) has usually been dismissed as abnormal.

The present paper is first a description of the larval development of *Palaemonetes pugio* Holthuis based on observations of larvae reared in the laboratory. The larvae and the development are compared to that of *Palaemonetes vulgaris* (Say) reared concurrently. Finally, the considerable variation in the number and structure of larval intermolts, found in the development of both species, is described.

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METHODS

Mature adult *P. pugio* and *P. vulgaris* are abundant in the vicinity of the Duke University Marine Laboratory at Beaufort, N. C., from late April until mid-October. Egg-bearing females were caught in dip nets and held individually in dishes of sea water in the laboratory until the eggs hatched, after which they were preserved for later identification and reference.

Groups of 10 newly-hatched larvae, all from the same clutch of eggs, were placed in clean four-inch finger bowls of sea water. The water was changed only if evidence of cloudiness appeared. The bowls of larvae were placed near north windows but not in direct sunlight. Because of other experiments which required constant illumination in an adjacent part of the laboratory, the room was never completely dark. No method of controlling the temperature of the building was available during the summer months. Most of the larvae were reared at temperatures which ranged from about 25 to 27° C. and none at lower than 20° C.

The diet of each larva was the same during its lifetime, but a variety of different foods or combinations of foods was offered to various larvae. Some were not fed. Other individuals received daily rations of either a species of unicellular algae, or a combination of species. Algae used included two species of *Nitzschia* and one species of each of the following genera: *Chlamydomonas*, *Thorocomonas*, *Nannochloris*, *Porphyridium* and *Pyramimonas*. Some larvae were fed species of algae combined with zooplankton which had been obtained by net and first killed by immersion in distilled water to prevent the fortuitous inclusion of living larvae similar to those being studied. The diet of some other larvae consisted of freshly killed zooplankton alone. A few larvae were fed on chaetognaths removed from the plankton and some others were fed tiny bits of the visceral mass of the mud snail, *Nassarius obsoletus*. The remaining larvae were fed living *Artemia* nauplii. Food was added to the bowls and uneaten food was removed daily.

Each larva was inspected daily under the low power of a stereoscopic binocular microscope. A record of molting by each larva was kept. Only the presence of

all or a large part of an exuvium or cast exoskeleton was accepted as evidence that a larva had molted. Morphological changes in larvae established which individuals had undergone the molt.

Camera lucida drawings were made of entire living larvae which had been anesthetized with ethyl carbamate and placed on slides beneath supported cover slips. These preparations were then sealed with oil. Larvae lived for as long as two hours under observation. Individual appendages from alcoholic specimens were studied and drawn.

Finally, adult females from which larvae were obtained were identified after comparison with type and other material at the U. S. National Museum.

RESULTS

The number of individuals of each species which survived each of the several molts is given in Table I. Only those larvae which were fed diets containing some animal tissue were able to survive. The number of ecdyses and, conversely, the number of intermolts or so-called larval stages were not constant among individuals of the same species.

In general, the differences were slight and the similarities great between the larvae of *P. pugio* and those of *P. vulgaris*. In some instances, preserved larvae were identical. Among living larvae, however, a difference in the distribution of chromatophores on the ventral surface of the abdomen proved to be an invariable index to species. Larvae of *P. pugio* bear, on the sternites of abdominal somites

TABLE I

Number of larvae of Palaemonetes pugio and Palaemonetes vulgaris which survived each molt in the laboratory and the number of postlarvae obtained by metamorphosis.
Column headings indicate diet of larvae

Molt number	<i>Palaemonetes pugio</i>					<i>Palaemonetes vulgaris</i>			
	No food	Uni-cellular algae	Algae plus animal tissue	Animal tissue	<i>Artemia</i> nauplii	No food	Uni-cellular algae	Algae plus animal tissue	<i>Artemia</i> nauplii
0	60	280	608	732	100	80	100	667	390
1	42	162	491	464	92	0	1	30	324
2	0	0	143	177	87		0	15	282
3			77	84	87			13	261
4			54	70	85			11	227
5			47	50	82			11	191
6			37	36	82			9	149
7			29	28	69			8	131
8			24	25				8	
9			18	14				8	
10			17						
11			17						
Number postlarvae	0	0	16	6	65	0	0	6	122

2 and 3, pairs of chromatophores. The larvae of *P. vulgaris* bear chromatophores on the sternite of abdominal somite 3, but lack pigment spots on abdominal sternite 2.

Although the individual larvae and the general pattern of development of *P. pugio* are nearly identical to that of *P. vulgaris*, differences between individuals of the same age and molting history and differences in the duration and tempo of larval development were observed in each species. Larvae which passed through the greatest number of molts during development showed the least morphological change after each molt. The structural characteristics of the individual larva were more readily associated with its total length than with its age or the number of molts completed. Although larvae which were of the same age often differed from one another in extent of development completed, those of about the same size were quite similar in structure regardless of the age or previous molting history. All larvae were alike upon hatching. This similarity began to disappear after the second molt. Considerable variation was found after the third molt, but, at the end of larval development, all larvae again resembled one another. The sequence or order of developmental events was the same for all larvae. The number of steps or stages passed through varied.

Differences in the form of larvae were accompanied by variation in the actual rate of development. Larvae fed living *Artemia* nauplii usually metamorphosed at the seventh molt which occurred about two weeks after hatching. Others, however, required from two to four weeks and as many as 13 molts to complete larval development. The variation observed, therefore, was primarily one of tempo.

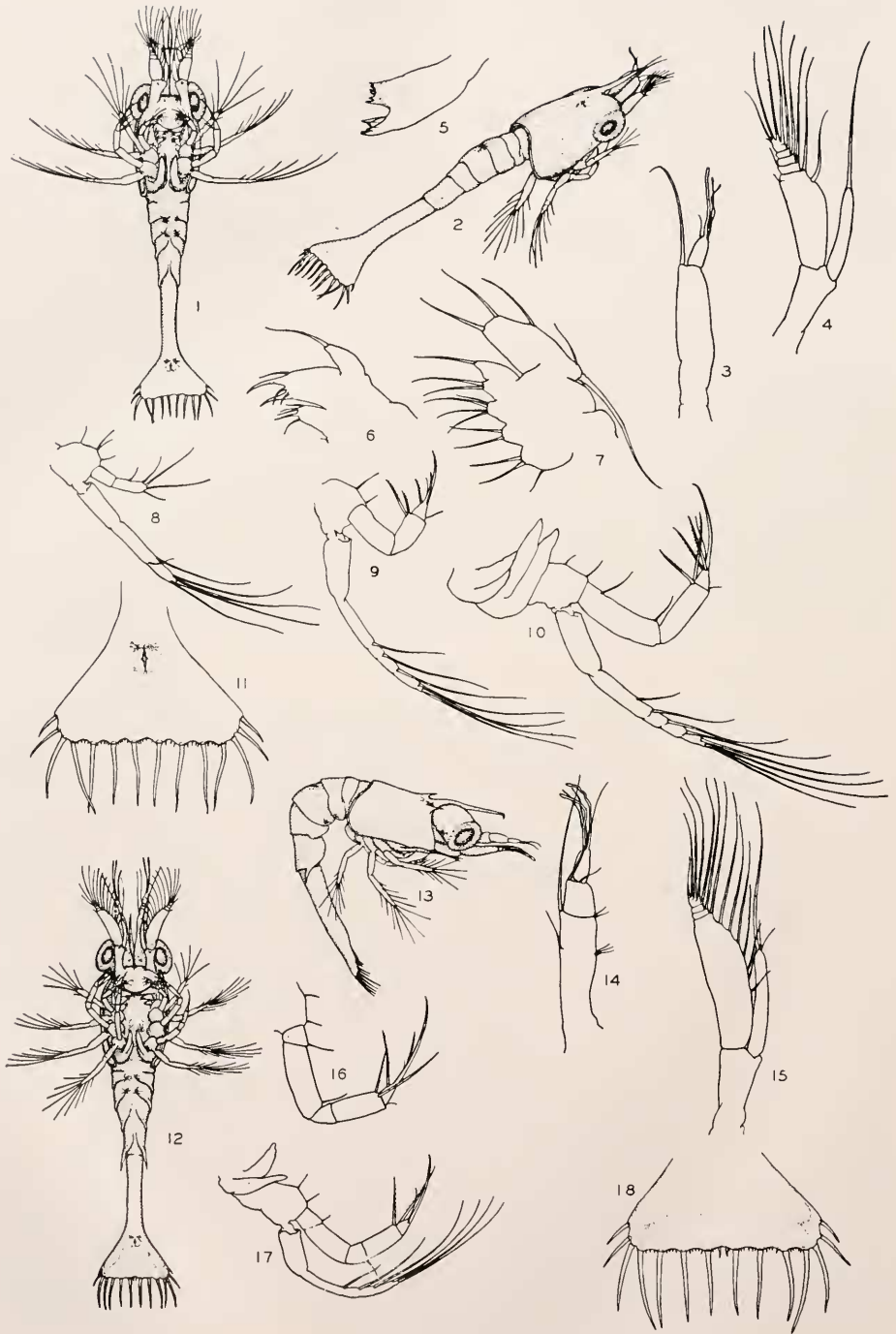
Larvae of Palaemonetes pugio

The eggs carried by adult females were from 0.5×0.6 to 0.6×0.9 mm. in size. They usually hatched within a few days, but always within two weeks or not at all. The prezoéal molt occurs immediately before hatching (Burkenroad, 1947), and the larva emerges from the egg as a zoea.

First zoea (Figs. 1-11): total length about 2.6 mm. Carapace, rostrum and abdomen without spines or teeth. Rostrum curved slightly downward at end. Abdomen of 6 somites, the last of which is not separate from the fan-shaped telson (Fig. 11). Telson with 14 spines. Eyes sessile, contained beneath carapace.

Antennule (Fig. 3) simple; the single basal segment bears terminally a long seta and a short outer flagellum; outer flagellum with three slender and one stout aesthetes and a short seta. Antenna (Fig. 4) biramous; basis unsegmented; flagellum of one segment, shorter than scale with a long terminal seta; scale of a long basal segment, which is convex on inner side, and four short terminal segments, with nine long setae on inner side and three short setae outside near tip.

Mandible (Fig. 5) without palp; incisor process with three teeth at tip; molar process with fine-toothed cutting edge; two movable teeth in angle between molar and incisor processes. First maxilla (Fig. 6) uniramous; coxa with five inwardly directed spines; basis with three spines and two teeth; endopod simple, palp-like, with a terminal seta. Second maxilla plate-like, biramous; protopod three-lobed, armed with three, two and four setae; endopod unsegmented, bears on a lobe near the proximal end two and terminally one setae; exopod a flattened gill bailer with three setae anteriorly, one laterally and one posteriorly.



First maxilliped (Fig. 8) biramous; coxa reduced; basis with four medially directed setae; endopod two-segmented, the distal segment with four terminal and one median setae; exopod longer than endopod with four apical and two sub-apical setae. Second maxilliped (Fig. 9) biramous; coxa reduced; basis with two setae; endopod three-segmented, with two strong spines at junction of ultimate and penultimate segments, ultimate segment with two smaller spines, a seta and a strong terminal claw; exopod longer than endopod with a cylindrical proximal and a flattened paddle-like distal segment which bears four apical and three pairs of sub-apical setae. Third maxilliped (Fig. 10) biramous, larger than second maxilliped, but generally similar to it; endopod with two setae on proximal segment; exopod with four apical and three or four pairs of sub-apical setae.

First and second pereopods (Fig. 10) rudimentary. Other appendages lacking.

Prominent groups of red and yellow-green chromatophores located dorsally at bases of eyes and at junction of abdominal somites 2 and 3. Paired groups of chromatophores ventrally on basal segment of antenna, on labrum, on thoracic sternites 1 and 8, on abdominal sternites 2 and 3 and on telson just anterior to anus.

This larva corresponds very closely to the first zoea of *P. vulgaris* and to Faxon's (1879) description of the first stage larva of that species. It differs from the larva of *P. vulgaris* chiefly in the presence of a pair of chromatophores on abdominal sternite 2, which are lacking from the latter species. The basal segment of the antennal scale of *P. vulgaris* is less convex on its inner side and the scale is narrower than in *P. pugio*.

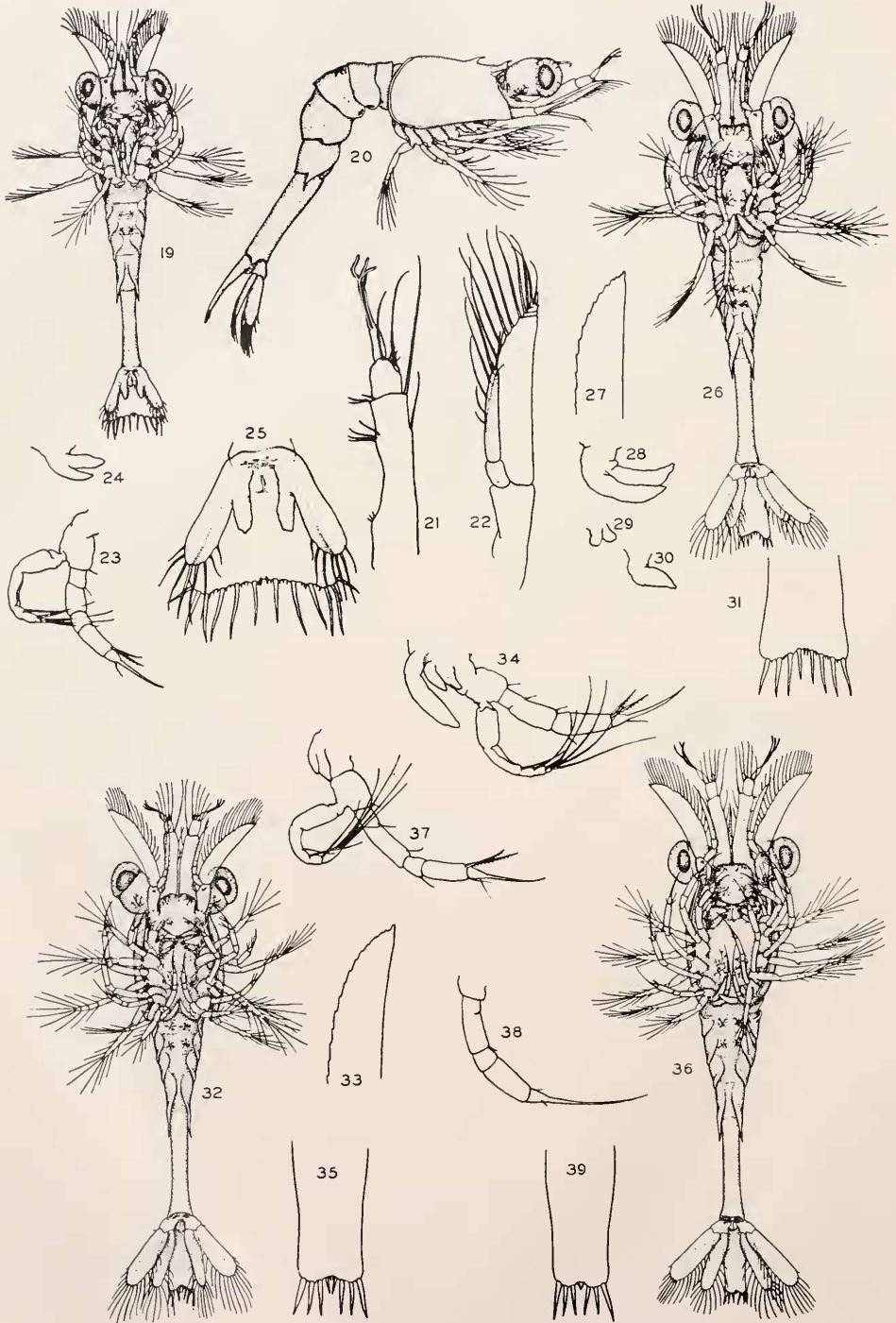
Second zoea (Figs. 12-18): length about 2.8 mm. Differs from first zoea in the following: Carapace with supra-orbital and branchiostegal spines. Rostrum recurved at tip and with one dorsal rostral tooth located on the carapace just behind orbit. Pleurum of fifth abdominal somite terminates as a posteriorly directed tooth. Telson (Fig. 18) with 14 large and two minute spines. The outlines of the uropods often visible within telson. Eyes stalked with chromatophores on postero-ventral side of stalk.

Antennule (Fig. 14) with peduncle segmented, segments marked by long setae on inner side, a long and a short seta on distal end of peduncle; outer flagellum with two slender and two stout aesthetes. Antennal scale (Fig. 15) with three short segments at the distal end and 14 setae; antennal flagellum terminates in a long and two short setae.

First maxilla with four teeth and three spines on basis. Exopod of second maxilla with five anterior setae. Endopod of third maxilliped (Fig. 16) five-segmented.

First pereopod (Fig. 17) biramous; coxa reduced; basis with two setae; endopod five-segmented, ischium, carpus and dactylus with a seta each, two stout spines at junction of propodus and dactylus, dactylus terminates in a strong claw; exopod as in third maxilliped.

PLATE I. Larval development of *Palaemonetes pugio*. Entire larvae $\times 19$; appendages $\times 54$. Figures 1-11 of first zoea. Fig. 1: ventral view. Fig. 2: dorsolateral view. Fig. 3: antennule. Fig. 4: antenna. Fig. 5: mandible. Fig. 6: first maxilla. Fig. 7: second maxilla. Fig. 8: first maxilliped. Fig. 9: second maxilliped. Fig. 10: third maxilliped and first and second pereopods. Fig. 11: telson. Figures 12-18 of second zoea. Fig. 12: ventral view. Fig. 13: lateral view. Fig. 14: antennule. Fig. 15: antenna. Fig. 16: endopod of third maxilliped. Fig. 17: first and second pereopods. Fig. 18: telson.



The second zoea corresponds to the second zoea of *P. vulgaris* and to Faxon's description of the second stage larva of that species. The second zoea of *P. vulgaris* differs from the corresponding larva of *P. pugio* in lacking chromatophores on abdominal sternite 2. All larvae which had molted once were in the form described.

Third zoea (Figs. 19–25): total length about 3.2 mm. Differs from the previous larva in the following: Sixth abdominal somite separate from telson. Telson (Fig. 25) narrower than before, armed with 12 large and two small spines.

Antennular peduncle (Fig. 21) with two long setae ventro-distally, two long setae on inner side, and, on a protuberance near the proximal end which will be the stylocerite, three short setae; a rounded prominence bearing three or four short setae and located dorsally near the distal end of the peduncle is the antennular lobe; outer flagellum with three stout aesthetes. Antennal scale (Fig. 22) with two short segments at distal end and 15 setae; antennal endopod separated into a short peduncle and an unsegmented flagellum which terminates in two short and two minute setae.

Second pereopod (Fig. 23) biramous; coxa reduced; basis with at least one seta; endopod five-segmented, first and last segments with setae, two stout spines arise from junction of propodus and dactylus, dactylus terminates in a strong claw; exopod shorter than endopod, similar in structure to other thoracic exopods. Third pereopod (Fig. 24) biramous, rudimentary.

Uropod (Fig. 25) biramous, unsegmented, with rudimentary inner ramus; outer ramus with 7 or 8 setae.

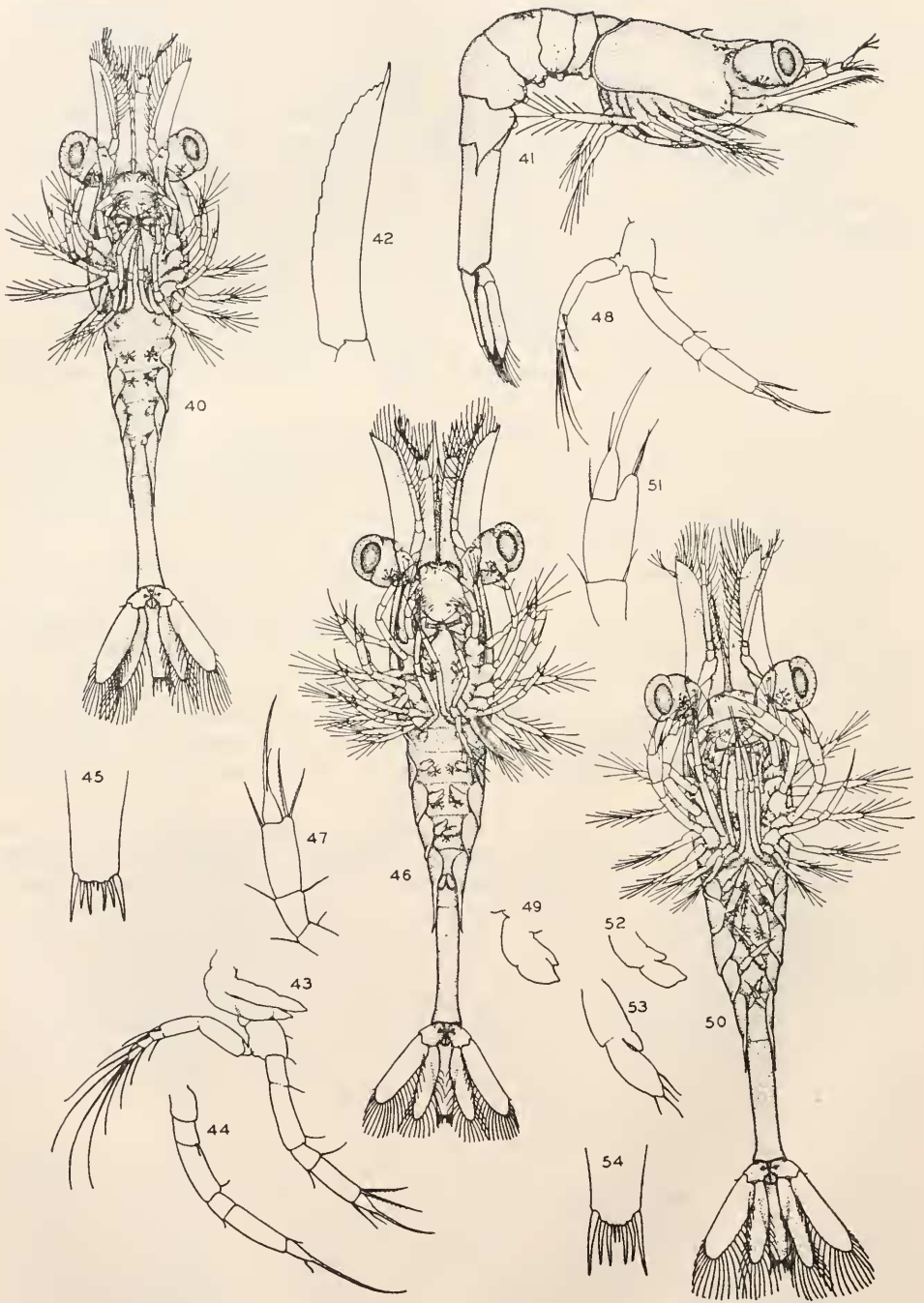
The third zoea corresponds to the third zoea of *P. vulgaris* and to Faxon's third stage. It differs from the third zoea of *P. vulgaris* in the presence of chromatophores on abdominal sternite 2. Variation in the form of larvae which had molted twice was noted in the total length and in the number of rudimentary pereopods present. Larger larvae had, in addition to the appendages described above, rudiments of third and fourth pereopods. All larvae which had molted twice were third zoeae.

Fourth zoea (Figs. 26–31): length about 3.5 mm. Differs from the third zoea in the following: Two dorsal rostral teeth on the carapace. Telson (Fig. 31) but little wider posteriorly than anteriorly, armed with eight stout and two small spines.

Antennular peduncle with four long distal setae and a protuberance which is the rudiment of the inner flagellum. Antennal basis separated into two segments by an oblique fissure at the articulation of the peduncle; scale (Fig. 27) not segmented, its disto-lateral tip (spine) projecting slightly, blade with 16 or 17 setae.

Second pereopod larger than before. Third and fourth pereopods (Figs. 28 and 29) biramous, rudimentary. Fifth pereopod (Fig. 30) uniramous, rudimentary. Uropod biramous; basis unsegmented; endopod shorter than exopod bears 8 setae; exopod with 12 setae.

PLATE II. Larval development of *Palaemonetes pugio*. Entire larvae $\times 19$; appendages $\times 54$. Figures 19–25 of third zoea. Fig. 19: ventral view. Fig. 20: lateral view. Fig. 21: antennule. Fig. 22: antenna. Fig. 23: second pereopod. Fig. 24: third pereopod. Fig. 25: uropods and telson. Figures 26–31 of fourth zoea. Fig. 26: ventral view. Fig. 27: tip of antennal scale, setae omitted. Fig. 28: third pereopod. Fig. 29: fourth pereopod. Fig. 30: fifth pereopod. Fig. 31: end of telson. Figures 32–35 of fifth zoea. Fig. 32: ventral view. Fig. 33: tip of antennal scale, setae omitted. Fig. 34: third, fourth and fifth pereopods. Fig. 35: telson. Figures 36–39 of sixth zoea. Fig. 36: ventral view. Fig. 37: third and fourth pereopods. Fig. 38: fifth pereopod. Fig. 39: telson.



The fourth zoea of *P. pugio* corresponds to the fourth zoea of *P. vulgaris* but has no equivalent in Faxon's descriptions of the larvae of that species. The fourth zoea of *P. pugio* differs from that of *P. vulgaris* in the distribution of abdominal chromatophores and in the projecting tip of the spine of the antennal scale, which, in *P. vulgaris* larvae, does not extend beyond and free of the blade. Not all larvae which had molted three times correspond to the fourth zoea as described here. Among those larvae which molted the least number of times during development, this form was not represented by any intermolt.

Fifth zoea (Figs. 32–35): total length about 3.5 mm. The fifth zoea differs from the fourth in the following: Telson (Fig. 35) narrower posteriorly than anteriorly, armed with six stout and two slender spines. Antennular peduncle with 5 long setae distally; inner flagellum a separate segment tipped with a short seta. Antennal scale (Fig. 33) with 19 setae, tip projecting; flagellum divided into a short proximal and a longer distal segment.

Mandible with three serrate movable teeth. Basis of first maxilla with five teeth and three setae. Middle lobe of basis of second maxilla with three setae; exopod with six to seven anterior setae.

Third pereopod (Fig. 34) biramous; coxa reduced; basis with at least one seta; endopod five-segmented, ischium, merus, carpus, and dactylus with setae, two stout spines at junction of propodus and dactylus, dactylus terminates in a claw; exopod shorter than endopod with four apical and two pairs of sub-apical setae. Fifth pereopod longer than fourth (Fig. 34), both rudiments. Uropodal endopod nearly as long as exopod, with 13 setae; exopod with a short seta on outside near proximal end and a short tooth in dorso-lateral corner, with 16 long setae.

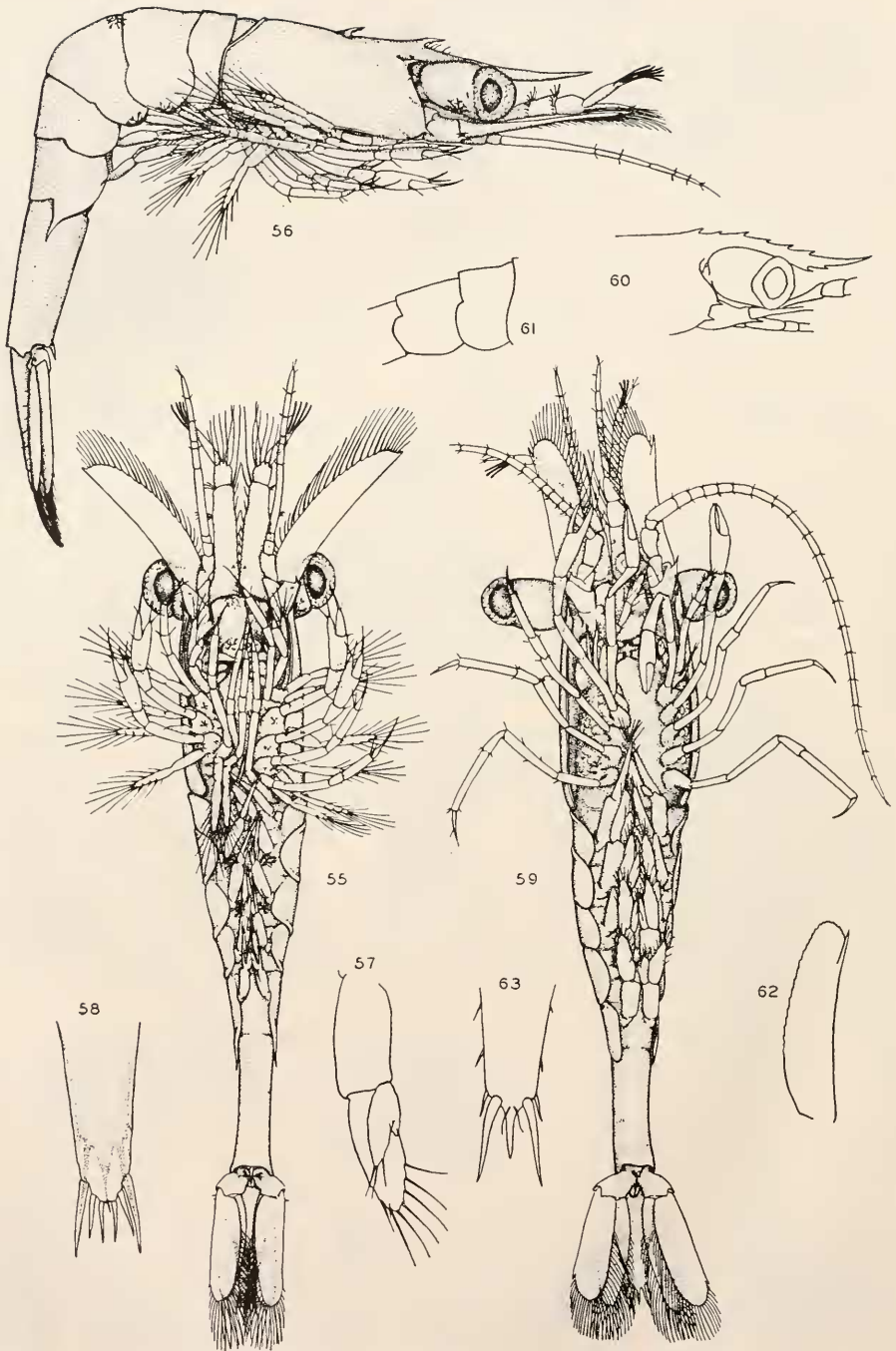
The fifth zoea of *P. pugio* differs from the fifth zoea of *P. vulgaris* as do fourth zoeae. There is no corresponding larval stage in Faxon's account of development of *P. vulgaris*, but a larva of this form was obtained by molt and considered abnormal by Faxon. This form may be skipped in the development of either species.

Sixth zoea (Figs. 36–39): total length about 3.7 mm. Differs from the previous larva in the following: Antennular peduncle with three plumose setae on inner side, angle of stylocerite is acute. Antennal scale with 20 plumose setae. Fifth pereopod (Fig. 38) uniramous; coxa reduced; short setae on merus, propodus and dactylus, dactylus terminates in a long claw. Uropodal exopod with 16, endopod with 13 or 14 setae.

The form described as the sixth zoea may be present in the development of either *P. pugio* or *P. vulgaris*. The species differ in the ways previously discussed. This form is not represented among Faxon's larval stages, but was seen by him and considered abnormal. This form may be skipped in the development of either *P. pugio* or *P. vulgaris*.

Seventh zoea (Figs. 40–45): total length about 4.4 mm. The seventh zoea

PLATE III. Larval development of *Palaemonetes pugio*. Entire larvae $\times 19$; appendages $\times 54$. Figures 40–45 of seventh zoea. Fig. 40: ventral view. Fig. 41: lateral view. Fig. 42: antennal scale, setae omitted. Fig. 43: third and fourth pereopods. Fig. 44: fifth pereopod. Fig. 45: telson. Figures 46–49 of eighth zoea. Fig. 46: ventral view. Fig. 47: first cheliped. Fig. 48: fourth pereopod. Fig. 49: second pleopod. Figures 50–54 of ninth zoea. Fig. 50: ventral view. Fig. 51: first chela. Fig. 52: first pleopod. Fig. 53: second pleopod. Fig. 54: telson.



differs from the sixth in the following: A minute anal spine present. Antennular peduncle with five setae on inner side; outer antennular flagellum with three stout and one slender aesthetes. Antennal scale (Fig. 42) with 20 setae. Fifth pereopod with a seta on each segment.

First to fifth pleopods represented by small uniramous buds.

The seventh zoea of *P. pugio* differs from the seventh zoea of *P. vulgaris* as the sixth zoeae differ and in regard to a small tooth on the ventral side of the antennular peduncle of the latter species. This tooth appears later in the development of *P. pugio* and is smaller than in *P. vulgaris*. Considerable variation in the development of the last three pereopods was found in larvae first having pleopod buds. Among those larvae which, in their development, had skipped the forms described as fourth, fifth and sixth zoeae, pereopods 3, 4 and 5 were rudiments. Among other larvae pereopod 5 was still rudimentary at the time of the appearance of pleopod buds. The seventh zoea described here corresponds most closely to Faxon's fourth larval stage of *P. vulgaris*. Larvae of either species may have molted three, four, five or six times when the form described as the seventh zoea is achieved.

Eighth zoea (Figs. 46-49): total length about 4.9 mm. The eighth zoea differs from the previous larva in the following: The anal spine is stronger. The antennular peduncle bears, about mid-way of the proximal segment on the ventral side, a small tooth, 7 setae on inner side, 6 setae at distal end. Antennal basis with a tooth on ventral side at junction of scale; scale with 23 setae; flagellum of three or four segments.

Propodi of first and second pereopods (Fig. 47) swollen and protuberant at inner distal corner, forming, with dactylus, the beginning of a chela. Fourth pereopod (Fig. 48) biramous; coxa reduced, basis with a seta; endopod five-segmented, ischium, merus and dactylus with one seta each, carpus with two setae, junction of propodus and dactylus with three spines, dactylus tipped with a claw. Fifth pereopod with a short spine arising from the middle of dactylus.

First to fifth pleopods (Fig. 49) small, biramous, rudimentary. Uropodal exopod with 20, endopod with 18 setae.

The eighth zoea of *P. pugio* corresponds to the eighth zoea of *P. vulgaris* from which it differs in the ways previously stated. This form corresponds to Faxon's fifth larval stage of *P. vulgaris*. There was considerable variation in the development of the pleopods, but all had non-setose, biramous pleopod rudiments.

Ninth zoea (Figs. 50-54): length about 5.1 mm. Differs from the previous larva in the following: Rostrum setose in the angle of the anterior tooth. Outer antennular flagellum with four equal, sub-apical aesthetes and a slender aesthete arising from mid-way of the segment. Antennal flagellum longer than scale, five-segmented; scale with 26 plumose setae. Entire outer edge of exopod of second maxilla setose. First maxilliped with a simple epipod, basal portion enlarged with 8 setae, proximal segment of exopod with two setae.

PLATE IV. Larval development of *Palaemonetes pugio*. Entire larvae and postlarva $\times 19$; larval appendages $\times 54$. Figures 55-58 of tenth (last) zoea. Fig. 55: ventral view. Fig. 56: lateral view. Fig. 57: second pleopod. Fig. 58: telson. Figures 59-63 of postlarva. Fig. 59: ventral view. Fig. 60: lateral view of rostrum and anterior portion of cephalothorax, $\times 19$. Fig. 61: lateral view of fourth and fifth abdominal pleurae, $\times 19$. Fig. 62: antennal scale, setae omitted, $\times 19$. Fig. 63: telson, $\times 54$.

First and second pereopods chelate (Fig. 51), the fixed finger tipped by the two spines formerly located at junction of propodus and dactylus. First to fifth pereopods with arthrobranchs.

First to fifth pleopods biramous. First pleopod (Fig. 52) rudimentary. Second (Fig. 53) to fifth pleopods with sparsely setose exopods. Uropodal exopod with 24, endopod with 17 setae.

The ninth zoea of *P. pugio* differs from the ninth zoea of *P. vulgaris* as previously described. The ninth zoea corresponds to Faxon's stage 6, first intermolt. Variation was noted in the extent of development of the inner ramus of the pleopods, the recurvature of the rostral tip, and the extent of development of the chelae.

Tenth zoea (Figs. 55-58): total length about 6.3 mm. The tenth zoea is the form representing full larval development. It differs from the previous larva in the following: Tip of rostrum curved slightly upward. Telson (Fig. 58) slender posteriorly, armed as before. Inner antennular flagellum with six aesthetes and two short apical setae. Antennal flagellum of 7 segments; scale with 30 setae, its tip projecting or not. Mandible with four or five movable teeth in angle between incisor and molar processes. Basis of first maxilla with 6 teeth. Exopod of second maxilla fringed with 29 setae.

Basis of first maxilliped with 9 setae and a bilobed epipod; proximal segment of exopod with 5 or 7 setae. Pereiopods essentially as before.

First pleopod with rudimentary endopod. Second (Fig. 57) to fifth pleopods biramous with setose exopods and endopods; endopods with small *appendices internae*. Uropodal exopod with 29 and endopod with 26 plumose setae.

The tenth zoea of *P. pugio* differs from the tenth zoea of *P. vulgaris* chiefly in the chromatophores of the ventral abdomen as previously discussed. This form corresponds to Faxon's sixth larval stage, intermolts 2 and 3. Some variation in the extent of development of the *appendices internae* of the pleopod endopods was noted.

Postlarva (Figs. 59-63): length about 6.2 mm. Rostrum shorter than antennal scale, with six dorsal teeth, the first of which is on the carapace directly over the posterior margin of the orbit, and two ventral teeth, the first of which is directly beneath the last dorsal tooth; tip of rostrum free of teeth (Fig. 60). Carapace with antennal and branchiostegal spines. Posterior margins of abdominal pleurae rounded (Fig. 61). Anal spine present. Telson (Fig. 63) with a tooth extending back from the mid-point posteriorly, two pairs of terminal spines of which the inner pair are longer, a pair of setae mid-ventrally near the distal end, and two pairs of dorso-lateral spines about $\frac{1}{2}$ and $\frac{3}{4}$ of the way from the proximal end.

Antennular peduncle of three segments; stylocerite less than $\frac{1}{2}$ the length of the basal segment of peduncle; antero-lateral spine of basal segment exceeding anterior margin of segment; inner side of peduncle with 10 setae; basal segment containing a statocyst and a short ventral tooth. Inner antennular flagellum simple, five-segmented. Outer antennular flagellum four-segmented, bearing on the anti-penultimate segment two, and on the penultimate segment three aesthetes, and a tuft of setae on the ultimate segment. Length of antennal scale (Fig. 62) about four times its width, outer margin slightly concave; anterior end of spine projects free of blade and is slightly shorter. Antennal flagellum over half of total length.

Mandible strong, incisor process stouter than in larval mandible; teeth of molar process large, forming a triangular surface, with or without movable teeth in angle.

Basal portion of first maxilla bilobed, each lobe bearing on its inner surface numerous coarse setae; endopod palp-like. Basal portion of second maxilla bilobed, each lobe bearing on its inner surface numerous coarse setae; endopod unsegmented with neither lobes nor setae; exopod setose around edge.

Basal portion of first maxilliped large, bilobed, the lobes with coarse setae directed inwardly; endopod reduced, bears two apical setae; exopod with six setae on proximal segment and four long setae at tip of distal segment; epipod large, bilobed. Second maxilliped with five-segmented endopod, ultimate and penultimate segments wider than long, armed with coarse spines; exopod with two setae; epipod small, bilobed. Third maxilliped with four-segmented endopod, coarsely setose throughout; endopod reduced; epipod tiny, bilobed.

First pereiopod chelate, somewhat stouter and shorter than second pereiopod; exopod a rudiment or lacking. Second pereiopod chelate, cutting edges of chela without serrations or teeth. Carpus shorter than palm; exopod rudimentary if present. Third, fourth and fifth pereiopods not chelate, exopods rudimentary if present. Arthrobranchs at bases of pereiopods.

Endopod of first pleopod rudimentary. Endopods of pleopods 2 to 5 with *appendices internae*. Uropodal exopod sparsely setose along outer edge with a tooth and a movable spine in the disto-lateral corner, numerous setae around the tip and on inner edge; endopod with setae on inner edge and around tip.

The distinctive distribution of chromatophores which characterized the larva is lost in the postlarva. The young prawn appears colorless to the unaided eye, but actually has numerous tiny chromatophores on the cephalothorax and abdomen. The postlarva of *P. pugio* is strikingly similar to the postlarva of *P. vulgaris*. The characters used to separate adults of these species are undeveloped in postlarvae. No attempt is made here to offer characters by which the two species may be distinguished at this stage of development. The postlarva corresponds to Faxon's seventh stage.

The sequence of larval intermolts

The descriptions of zoea larvae given above were based on the structure of individuals reared in the laboratory. Since the number of molts during development is not constant, it is obvious that certain of the described forms may be omitted in the life history of any individual. The relationship between the number of molts and the structure of intermolts observed in the laboratory is given in Table II. Column 4 of Table II shows that, for some larvae, the sequence of successive intermolts was that given in the text descriptions. Columns 5 to 9 show progressive omission of more of the described forms. The data suggest a relationship between diet and the number and form of larval intermolts.

DISCUSSION

Larvae of *Palaemonetes* reared in the laboratory were structurally identical to those from nature described by Faxon (1879). This resemblance extended even to certain larvae considered abnormal by Faxon but shown by rearing to belong to series of intermolts which ultimately metamorphosed to produce normal postlarvae. The distinctive distribution of abdominal chromatophores, which was found to be diagnostic for the species treated in this paper, was not noted by Faxon

TABLE II

The relationship between molting and form of *Palaemonetes pugio* and *Palaemonetes vulgaris* larvae fed various diets. Numbers in column 1 refer to text descriptions. Numbers in parentheses refer to described variations. The sequence of forms through which larvae pass in development is given in columns 4 to 9.

Zoea larva No.	Approx. total length (mm.)	Recognition character	Non-living animal plus unicellular algae		Intermolt number Non-living animal		<i>Artemia</i> nauplii	
1	2.6	Sessile eyes	1	1	1	1	1	1
2	3.0	Stalked eyes	2	2	2	2	2	2
3	3.2	Telson and uropods	3	3	3			
(3)	3.3	4th and 5th pereopod rudiments				3	3	3
4	3.5	2 dorsal rostral teeth	4	4	4	4		
5	3.5	3rd pereopod	5	5				
6	3.7	5th pereopod	6	6	5			
7	4.4	Pleopod buds	7	7	6	5	4	4
8	4.9	Pleopod rudiments	8		7	6		
(9)	5.0	Chelae		8			5	5
9	5.1	Pleopod exopod	9	9	8	7	6	6
10	6.1	Pleopod endopod	10			8	7	
(10)	6.3	Appendices internae	11	10	9	9	8	7
PL	6.3	Postlarva	12	11	10	10	9	8

who found pigment spots to be variable in position. Minor morphological details, which might serve as indices of species, were not discussed or figured by Faxon. It seems possible that he may have dealt with larvae of more than a single species, although Holthuis (1952) feels that the adults and, presumably, the first stage larvae described by Faxon were *P. vulgaris*.

The normality of larvae reared in the laboratory has been questioned by Gurney (1942) who believes that abnormal stages may be reared under artificial conditions. Gurney further states, however, that "extra stages," through which each individual need not pass in development, occur in nature. Numerous references to these extra stages are available (Faxon, 1879; Gurney and Lebour, 1941; Lebour, 1940).

Fraser (1936) and Boden (1950, 1951) defined stages or norms of variation in euphausiid *Furcilia* larvae on the basis of the frequency of occurrence of all the forms encountered. As a result of these analyses it is possible to state that some of the forms are normal and some abnormal in a purely statistical sense. No treatment of the frequency of occurrence of variation in larvae of a decapod is available. It is not presently possible to state with certainty that any individual decapod larva is either normal or abnormal except on the basis of the course of its development. Defining normal development, however, presents great difficulties. MacDonald (1927) and Fraser found numerical predominance of certain of the euphausiid *Furcilia* stages over others. It was assumed that certain of the stages may be skipped in development. This assumption was confirmed by Fraser in the laboratory. The normality of individual larvae and the course of larval development possibly depends upon extrinsic factors. Sandoz and Rogers (1944) found optimum temperature and salinity conditions for molting of *Callinectes* larvae and that the tempo of molting might be reduced by a sub-optimal diet. In view of the

lack of evidence to the contrary, the variation observed in the structure of larvae and the tempo of development in *Palaemonetes* is considered to be within the limits which may be considered normal for the species.

The apparent discrepancy in the proposed developmental sequence, shown by the unfolding of pereopods 3 and 5 before the appearance of pleopods in some larvae and after the pleopod buds have been formed in others, may be a function of rate rather than sequence of development. Pereiopod 3 appears after the second molt and is followed by pereopods 4 and 5. These may appear all at once in the third intermolt among rapidly developing larvae, or their appearance may be in separate intermolts. All the fourth intermolt larvae have five pairs of pereopods of which the last three are rudimentary. Among rapidly developing larvae the pleopod buds appear in the fourth intermolt, before the last three pereopods have unfolded. If pleopods do not appear in fourth, fifth or sixth intermolt larvae, pereopods 3 and 5 will have become functional before the pleopod buds are first seen. Pleopods always follow pereopods in appearance. The length of time or number of intermolts which intervene may permit some variation in the status of pereopod unfolding at the time of the pleopod appearance.

The present concept of the crustacean larval stage has contributed to confusion regarding development. Most authors refer to each larval intermolt as a stage. Numbers are assigned to these stages which presume a knowledge of the molting history of the individual. Thus, a larva is assumed, on the basis of structure alone, to have molted a certain number of times and, presumably, to be of a certain age. The basis for this implication is an assumed norm of development on which reasonable doubt may be cast.

Development in arthropods is made to appear discontinuous by the inflexibility of the exoskeleton during the intermolt period. The morphology of the individual larva, which cannot change during the intermolt period, is determined by the extent of development completed at the time of the last molt. Fraser (1936) feels that, within limits, the time of molting may shift slightly backwards and forwards. This fluctuation, superimposed on a continuous process of development, was suggested as the cause of variation in euphausiid larvae. Heegaard (1953) has suggested variation in the rate of larval development in penaeids, but did not discuss molting. No variation in larvae is possible if either a causative or a casual relationship between molting and development exists so that each larval molt occurs at a precise time in development. The presence of larvae of the same molting history which vary widely in size and form argues in favor of the independence of the frequency of molting from the rate of larval development.

Arbitrary stages may be defined in crustacean development but should not be thought of as inflexible, natural steps through which each individual passes. The choice between few or many stages is possible. If, as has frequently been the case, each form found is described as a stage, then many individuals may skip certain stages in development. If few stages are defined, certain individuals may pass through what might be called extra stages during the course of normal development.

The inference that the variation in tempo of larval development is related to diet is inescapable. Trophic conditions may vary in nature during the breeding season of each species. At Beaufort, *Palaemonetes* larvae hatched in late April or May become part of a plankton community which is poor in total number of

organisms. A possible response to this sub-optimal condition might be prolonged larval life with a greater number of larval intermolts. Normal development of a decapod may itself vary according to the season of the year.

SUMMARY

1. *Palaemonetes pugio* Holthuis and *Palaemonetes vulgaris* (Say) were reared in the laboratory from eggs through metamorphosis.
2. The larvae of these species are very nearly identical except for a pair of chromatophores found on abdominal sternite 2 of *P. pugio* but lacking from *P. vulgaris*. The sequence of development is the same for each species.
3. Individual larvae which were of the same age or which had molted the same number of times were not necessarily alike. Larvae of the same size, regardless of age or the number of molts completed, were alike. This discrepancy between age and development seems associated with the diet of the larvae.
4. The molting frequency of the larvae was independent of the rate of development.
5. Descriptions of a series of *P. pugio* larvae which illustrate the sequence of events in larval development are given. Some of these forms may be skipped.
6. The concept of the crustacean larval stage has assumed a constancy of development at variance with the facts observed in rearing experiments. The form of a larva alone may not be regarded as indicative of its age or previous molting history.

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